

Limpet Radulae: The Relationship Between Intertidal Height and Radula Length in Temperate and Tropical Limpets

by

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Abstract. The relationship between radula length and height occupied intertidally was investigated in several species of limpets in British Columbia and Barbados. Radulae were significantly longer in high-level individuals as compared with low-level ones in *Tectura persona*, *Acmaea jamaicensis*, and *A. leucopleura*, but not in *Lottia digitalis* or *T. scutum*. The extent of such intraspecific difference in radula length may be related to the degree of homesite fidelity exhibited by a species which, in turn, limits the feeding opportunity of high- and low-intertidal members of a population. Results of a field translocation experiment to test the effect of feeding time on radula length led to inconclusive results, but a parallel laboratory tide-tank experiment offered support for the idea that food availability and feeding opportunity may be important in regulating radula length.

INTRODUCTION

Limpet radulae are best known for their taxonomic importance, but are also of ecological interest. Radula fraction (defined as radula length over shell length; FISCHER-PIETTE, 1935) was initially investigated as a taxonomic character in *Patella* spp. by EVANS (1947) and BRIAN & OWEN (1952). However, the classificatory value of this ratio was dismissed in the latter study owing to its marked intraspecific variation and an apparent correlation between radula fraction and the animal's intertidal position. BRIAN & OWEN (1952) showed that the radula fraction of high-level *P. vulgata* at five sites on the west coast of Great Britain was greater than that of lower-level conspecifics, confirming a pattern reported earlier by EVANS (1947), and EBLING *et al.* (1962), for *Patella* spp. and later documented by RAO & GANAPATI (1967) for *Cellana radiata*.

Intertidal-level differences in radula fractions of limpets, as defined by the above authors, can represent the combination of two contrasting tendencies: (1) a decrease in shell length with increasing intertidal height, possibly caused by desiccation stress (ORTON, 1932; MOORE, 1934; EBLING *et al.*, 1962; VERMEIJ, 1973; SIMPSON, 1985) and

(2) an increase in radula length with increasing tidal height owing to a presumed decrease in radula wear as limpets at higher levels have less immersion time in which to feed. Neither tendency individually caused statistically significant differences in shell or radula length in the study of *Patella vulgata* by BRIAN & OWEN (1952), and there has been dispute among past investigators as to which factor contributes most to an observed tidal height-related change in radula fraction.

It is the purpose of the present study to reinvestigate the relationship between intertidal height and radula fraction in limpets. To this end a correlate of radula length that is not independently affected by tidal height was sought as a replacement for shell length in the definition of radula fraction. Possible correlates such as shell height, width, volume, and dry weight of soft tissues were investigated for the limpet *Tectura persona* in British Columbia. The relationship between intertidal height and radula length was studied in this species, in *Lottia digitalis*, and in *T. scutum*, as well as in the Caribbean species *Acmaea leucopleura* and *A. jamaicensis*. The effect on radula length of reciprocal translocations of limpets from high to low intertidal positions was studied in *T. persona* using field cages and a laboratory tide-tank. Finally, the relation of radula length to extent of vertical movement undertaken by a limpet species was investigated in three acmaeid species in

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Barbados, *A. leucopleura*, *A. jamaicensis*, and *A. antillarum*, which exhibited various degrees of homesite "attachment." (Note: there is confusion regarding the taxonomic status of Caribbean limpets [D. Lindberg, personal communication], especially with regard to possible synonymy of *A. leucopleura* and *A. jamaicensis*. However, in the present study the three putative species occupied different habitats, lived at different intertidal heights, were of different size ranges, and showed differences in behavior especially with respect to homing.)

MATERIALS AND METHODS

Habitat Descriptions

Limpets were collected at two sites in British Columbia (January–March 1987) and at one site in Barbados, West Indies (May 1987). *Tectura persona* was collected at Lighthouse Park near Vancouver, British Columbia, a semi-protected rocky area consisting of tumbled boulders extending from a vertical rock-face. *Lottia digitalis* and *T. scutum* were collected from a site near the Bamfield Marine Station on the west coast of Vancouver Island, British Columbia. In this region *L. digitalis* occupied a wave-exposed vertical rock-face, while *T. scutum* was found among tumbled rocks in a more sheltered area. At all British Columbia sites the food available to the limpets consisted of benthic diatoms and small epilithic red and green algae, more abundant at the lower intertidal levels during summer (see also PHILLIPS, 1981), but more evenly distributed throughout the intertidal zone during winter when a rich diatom growth was evident. The limpets were unevenly distributed. At the more wave-exposed Bamfield site, the population of *L. digitalis* was denser at higher intertidal levels. *Tectura persona* at Lighthouse Park were also in greatest abundance at higher intertidal levels. Larger individuals of both species tended to be found at higher parts of the distribution, and smaller ones at lower parts. This may represent an age segregation of the population, as has been noted in other studies (*e.g.*, BREEN, 1972). To eliminate size (age) effects as far as possible in the present study, we attempted to select animals of similar size ranges from the two intertidal levels. This was possible with most species, except *L. digitalis*, where the size disparity between high- and low-level inhabitants was greater. In any case, such size discrepancies were ultimately accounted for by a factoring design in the ANOVA which compared different sets of animals at a common size. The overall vertical range occupied by each population was as follows: *T. persona* (2.6–4.3 m above chart datum), *L. digitalis* (2.9–4.5 m), and *T. scutum* (1.0–2.9 m).

The tropical limpets *Acmaea jamaicensis*, *A. leucopleura*, and *A. antillarum* were collected from a coral limestone breakwater wall and adjacent boulder riprap at Six Men's Bay, on the west coast of Barbados. At this site, food available to the limpets consisted of diatoms, algal sporlings, and other unicellular and filamentous green algae.

The populations were distributed from about 0.20 to 0.85 m above chart datum, with *A. antillarum* occupying the lower portion and *A. jamaicensis* and *A. leucopleura* the upper portion, with total tidal range on spring tides in this region being about 1 m. Precise demarcation of intertidal distributions was made difficult by almost constant wave splash, even on fairly calm days. The size distribution of the three species was nearly equal throughout their vertical ranges, although for *A. jamaicensis* larger individuals tended to be found at the lower part of the distribution and smaller individuals at the upper part.

The three acmaeid species in Barbados exhibited graded degrees of homesite fidelity, from *Acmaea leucopleura*, which occupied distinctive homesite scars conforming in size to their shell dimensions, to *A. jamaicensis*, which showed some site fidelity (to depressions in the rock, not their own scars), to *A. antillarum*, which showed no site fidelity. Observations were made on individual *A. leucopleura* and *A. jamaicensis* to assess the extent of daily movements in total distance and, for the latter species, in net vertical distance. Individual animals were identified through scratch marks (*A. leucopleura*) or distinctive natural markings or growths (*A. jamaicensis*) on their shells. For *A. leucopleura*, orientation markings scratched on the rock surface adjacent to the home scar in line with the mark on the shell were used as reference points to determine whether animals had made foraging excursions. A limpet was judged to have moved if it was found in a different orientation in its scar or in a different scar; this was a minimum estimate because some animals may have made undetected excursions by returning to the same scar and orientation. In the case of *A. jamaicensis*, which lived on a vertical part of the rock wall, two reference nails were driven into the rock on which was hung a sheet of clear plastic where locations of animals were marked. Observations on site fidelity of *A. leucopleura* and *A. jamaicensis* were made on successive low tides over 15- and 10-day periods, respectively.

Radula Lengths

Lengths of radulae were recorded for most species from animals collected at their highest and lowest intertidal distributions. Where a species' distribution was exceptionally narrow as, for example, *Acmaea antillarum* in Barbados, animals were collected at a single tidal level. For a population of *Tectura scutum* at Bamfield, radula lengths were examined from a series of animals occupying different intertidal heights over a vertical range of 1.8 m.

Each limpet's radula was removed from the radula sac by pulling it out through an anterodorsal incision in the buccal mass. The intact nature of the organ was assured by the appearance of a clear end to the radula on which no cusps could be seen with a dissecting microscope. Radula length was taken as the total length procured by this technique. In addition to radula length, the following morphological characteristics were recorded from each dissected *Tectura persona*: (1) shell length, (2) shell width,

(3) shell height, (4) shell volume, and (5) dry tissue weight. Measures of body dimensions were done with vernier calipers. Weight-to-volume standardized sand was used to obtain shell volume. Dry tissue weight, including radula, was recorded for limpets removed from their shells and oven-dried to constant weight at 90°C. For the other limpet species, only shell length and dry tissue weight were determined. Although animals were starved for 2 days prior to dissection to clear their guts, some digested food remnants regularly remained in the posterior gut loops and were included, therefore, as tissue weight. A separate investigation showed that the magnitude of this error source was in fact small, the dried gut contents representing a mean of 1.6 ± 0.4 SE % of the total dry weight in high-level animals ($n = 11$, 40–320 mg dry tissue wt) and 2.8 ± 0.8 SE % in low-level animals ($n = 12$, 20–100 mg dry tissue wt).

Translocation Experiments

In order to assess the effect of a change in intertidal height on radula length a reciprocal translocation experiment was done in the field using *Tectura persona*. High intertidal-level animals were transferred to a low intertidal level and low animals to high. Control animals were maintained at their original intertidal heights. After a 10-week period (estimated to be long enough to allow the radula to change in length), the animals were dissected and radula length and body size data collected as before. Field cages, consisting of two mesh boxes ($0.5 \times 0.3 \times 0.2$ m height, aluminum mesh of 10-mm-opening size), were placed in the Lighthouse Park site 2.6 m above zero chart datum. Limpets were also barricaded into narrow, shallow crevices in the rock-face at 4.3 m tidal level, using similar aluminum mesh. Sixty animals were collected at each tidal height, divided into two groups of 30, and placed in the appropriate cages on rocks collected from the surrounding beach area. Thus, at each level, cages housed 30 animals from the high intertidal level and 30 from the low, with one set being the control, and the other, the experimental. After a 10-week period the animals were retrieved and their radulae removed.

In order to test more completely the assumption that radula wear is the main factor influencing radula length, an additional experiment was performed in a laboratory tide-tank. We hoped that the tide-tank would provide a more uniform environment than the field, a uniform environment in which all animals would feed off the same substratum which, owing to uniform illumination in the tank, would support similar types and amounts of algal growth. The experiment involved translocation of high-level *Tectura persona* to simulated high and low levels in the tank. The animals were kept in this tank on slate plates ($25 \times 25 \times 0.5$ cm thick) suspended at heights corresponding to their intertidal heights in the field. The laboratory tide-tank produced simulated semidiurnal tides of 1-m magnitude on a 24-h cycle (CAREFOOT, 1981). The

vertical separation of the plates was 0.34 m, equivalent to a separation of 1.7 m in the field. Several 60-W fluorescent bulbs were suspended above and in front of the tide-tank to promote algal growth on the slate plates. Prior to introduction of the animals into the tank, the plates supported a visible growth of diatoms and, after being placed on the plates, animals were observed to feed on this growth during immersion. No attempt was made to monitor the intensity of illumination or, except in a qualitative way, to assess the production and consumption of algal food on the plates. The experiment involved 60 animals collected from a high intertidal position in September and divided into two subgroups of 30 animals each. One subgroup of high intertidal-level animals, representing the control set, was placed on high-level plates in the tide-tank (15 animals per plate); the other subgroup, representing the experimental set, was placed on low-level plates. Animals were sampled at time 0, and then after 3 and 7.5 weeks in the tide-tank. In this way, we hoped to learn something of the time sequence involved in length changes in the radulae.

Data Analyses

Stepwise linear and logarithmic multiple regression analyses were done on regressions of radula lengths versus shell length, shell height, shell volume, and dry weight in *Tectura persona* in an attempt to identify the size variate giving the best correlation with radula length. In so doing, we hoped to identify a correlate of radula length that was not as independently affected by tidal height to substitute for shell length in the previous definition of radula fraction, and thus to develop a better means of correcting measures of radula length for animal size.

Log-transformed high- and low-level radula lengths were compared within and between species using two- and three-way analyses of variance (ANOVA), respectively, and multiple comparison tests (MCT, $\alpha = 0.05$), with weight factored out. The use of a factoring design in the analysis allowed size ranges of animals to be compared directly without resorting to a size-corrected "radula fraction" as used in previous studies (BRIAN & OWEN, 1952; RAO & GANAPATI, 1967). Some covariance analyses (ANCOVA) of slopes of regression lines were also performed.

RESULTS

Regression statistics for the relationship of radula length to various size dimensions of the body (shell length, width, height, and volume, and dry tissue weight) in *Tectura persona* are given in Table 1. Also included are regression statistics for the relationship of radula length to dry tissue weight for *Lottia digitalis*, *T. scutum*, *Acmaea leucopleura*, *A. jamaicensis*, and *A. antillarum*. Because it was initially unclear whether radula length would scale linearly with weight and volume dimensions, or whether a non-linear function would give the best fit, some of the data were fitted to both linear ($y = a + bx$) and logarithmic ($\log y$

Table 1

Regression statistics for the relationship of radula length to various shell parameters and dry tissue weight for several species of limpets. Linear regression equation: $y = a + bx$; logarithmic regression equation: $\log y = \log a + b \log x$.

Species	Intertidal position	Parameter measured	Regression type	a^\dagger	b	r	
<i>Tectura persona</i>	High	Shell length	Linear	-0.98	1.89	0.83	
		Shell width	Linear	-4.56	2.63	0.84	
		Shell height	Linear	5.39	4.32	0.85	
		Shell volume	Linear	23.64	16.64	0.78	
	Low	Dry weight		Logarithmic	0.64	0.38	0.84
				Linear	24.54	0.10	0.77
		Shell length		Logarithmic	0.87	0.35	0.83
				Linear	2.50	1.51	0.75
				Linear	4.46	1.74	0.67
		Shell height		Linear	11.59	2.62	0.75
				Linear	22.34	10.90	0.78
		Shell volume		Logarithmic	0.53	0.25	0.59
				Linear	21.37	0.09	0.78
			Dry weight	Logarithmic	0.89	0.31	0.77
<i>Lottia digitalis</i>	High	Dry weight	Linear	13.28	0.06	0.68	
			Logarithmic	0.72	0.29	0.69	
	Low	Dry weight	Linear	11.81	0.08	0.85	
			Logarithmic	0.74	0.28	0.87	
<i>Tectura scutum</i>	Mixed	Dry weight	Linear	27.67	0.04	0.81	
			Logarithmic	0.86	0.21	0.65	
<i>Acmaea leucopleura</i>	High	Dry weight	Linear	10.48	0.09	0.64	
			Logarithmic	0.80	0.22	0.66	
	Low	Dry weight	Linear	8.35	0.10	0.82	
Logarithmic			0.68	0.26	0.85		
<i>Acmaea jamaicensis</i>	High	Dry weight	Linear	9.29	0.10	0.57	
			Logarithmic	0.81	0.19	0.63	
	Low	Dry weight	Linear	8.51	0.09	0.61	
			Logarithmic	0.74	0.20	0.70	
<i>Acmaea antillarum</i>	Mixed	Dry weight	Linear	8.98	0.17	0.90	
			Logarithmic	0.47	0.46	0.81	

\dagger For logarithmic regressions, a is given in log form.

= $\log a + b \log x$) equations. For *T. persona*, r values ranged from 0.77 (dry weight) to 0.85 (shell height) for high-level animals, and from 0.59 (log shell volume) to 0.78 (dry weight and shell volume) for low-level animals. Overall, low intertidal-level *T. persona* showed greater variability in radula lengths in relation to the correlates tested than did high-level animals regardless of whether they were linearly or logarithmically expressed. A stepwise multiple regression analysis of the linear values showed that shell height and dry tissue weight accounted for most of the variance in radula length in high-level *T. persona* (t values of 2.935 and 1.074, respectively, d.f. = 17; but only shell height was significant: $t_{0.05(2), d.f. 17} = 2.110$), and shell volume and dry weight in low-level animals (t values of 3.165 and 4.741, respectively, d.f. = 17). A similar analysis on the logarithmic values resulted in no significant effect of any variable on radula length for high-level animals (t values < 0.416 , d.f. = 15, where $t_{0.05(2), d.f. 15} = 2.131$), but a highly significant effect of dry weight in low-level animals ($t = 4.596$, d.f. = 17). Overall, then, dry

weight accounted for the greatest effect on radula length of all parameters tested in *T. persona*. Also, because the correlation coefficients for logarithmic regressions of radula length and dry weight were mostly as high or higher than for the comparable linear regressions for all species, and because it would generally be expected that radula length would scale non-linearly with dry weight, the logarithmic relationship was accepted as the working model for *T. persona* and for the other limpet species in the present study.

In all instances where a limpet species showed strong homing tendencies (*Acmaea leucopleura* and *A. jamaicensis*) or remained at a relatively constant intertidal height (*Tectura persona*), radulae were longer in the high intertidal-level animals than in the low-level ones (Figure 1, Table 2; respective P values of < 0.001 , < 0.001 , and 0.01; ANOVA). For these three species, radula length of high-level animals was about 14% greater than that of low-level animals at a given weight. In comparison, neither *Lottia digitalis* ($P = 0.87$, ANOVA) nor *T. scutum* showed sig-

Table 2

Radula lengths in high- and low-intertidal limpets. The "common weight" is the factored dry tissue weight at which the ANOVAs were performed between high- and low-intertidal groups of the same species. Slopes of radula lengths versus dry weight of tissues did not differ significantly between high- and low-level groups for any species ($P > 0.50$, ANCOVA).

Species	<i>n</i>	Intertidal position	Height above chart datum (m)	Animal weight (\bar{x} dry mg \pm SE)	Common weight (dry mg)	Radula length at common weight (mm)	<i>P</i> (ANOVA)
<i>Tectura persona</i>	20	High	4.3	67.2 \pm 12.7	57.0	30.5	0.01
	20	Low	2.6	71.3 \pm 12.3		27.2	
<i>Lottia digitalis</i>	25	High	4.5	90.8 \pm 4.2	61.4	17.3	0.87
	25	Low	2.9	45.5 \pm 3.6		17.4	
<i>Acmaea leucopleura</i>	25	High	0.50	31.0 \pm 1.7	29.4	13.3	<0.001
	25	Low	0.20	33.0 \pm 3.2		11.5	
<i>Acmaea jamaicensis</i>	25	High	0.85	15.8 \pm 1.2	17.3	11.1	<0.001
	25	Low	0.20	22.6 \pm 2.1		9.7	

nificant intertidal-height effects (data for *T. scutum* presented in Figure 2 as the relationship between the ratio of radula length over dry tissue weight, to intertidal height occupied). Slopes of regressions of radula length on dry tissue weight did not differ significantly ($P > 0.50$, ANCOVA) between the high- and low-level groups for any species. Therefore, the differences shown by ANOVA are not due to size (age) effects, but rather to some other effect(s) (e.g., intertidal height).

Observations on the extent of homesite fidelity in *Acmaea leucopleura* and *A. jamaicensis* showed that while neither species moved very much, the former may have been more strongly "site-attached" (Table 3). Movements by *A. jamaicensis* were from one small depression in the rock to another, while movements of *A. leucopleura* were on and off "homesite" scars. Some *A. leucopleura* occupied more than one scar and movements were limited to these. Sixty-five percent of all observed day-to-day movements by this species terminated on the same scar, 35% on an alternative scar. Mean vertical displacements of the two species did not differ significantly from zero, nor did high- and low-level groups of *A. jamaicensis* differ significantly from one another (Table 3). Although precise data on vertical movements of *A. leucopleura* could not be obtained because of rough-water conditions and irregular rock topography, it was apparent from observations of marked individuals that vertical displacements were smaller in this species than in *A. jamaicensis*. Each species had radulae that were significantly longer in high intertidal-level animals (Table 2). However, the difference in radula lengths between high and low individuals was somewhat greater in *A. leucopleura* than in *A. jamaicensis* (16 and 14% differences, respectively), possibly reflecting the difference in homesite fidelity of the two species. Unfortunately, vertical movements of the low intertidal-level-inhabiting *A. antillarum* could not be monitored owing to difficulty in marking and, later, in locating individuals. Our observations, however, indicated that this species was much more free-ranging in

its low intertidal-level habitat than the other two. The radula length in this species was 14.1 mm ($n = 21$), somewhat greater than in *A. leucopleura* (12.2 mm, $n = 50$) and *A. jamaicensis* (11.5 mm, $n = 50$) at a common dry tissue weight of 30 mg (determined from regression equations).

The results of the translocation experiments on *Tectura persona* are given in Table 4. As predicted, change in intertidal height had a highly significant effect on radula length in this species ($P < 0.001$, ANOVA). The most obvious effect was on radula lengths of high- and low-level control animals, with the former possessing radulae about 15% longer than the latter (46.2 and 40.0 mm, respectively, measured at the common dry tissue weight of 148 mg at which the ANOVA was performed; $P < 0.05$, MCT). However, the predictions that radula lengths would be decreased through translocation of high-level animals to

Table 3

Extent of movements of acmaeid limpets in Barbados resulting in returns to homesite scars or depressions, and net daily displacements after feeding excursions over a high-tide cycle. Individuals of *Acmaea jamaicensis* were divided into high and low intertidal-level groups (separated here by a vertical distance of 30 cm) and were observed over a 10-day period; individuals of *A. leucopleura* were observed over a 15-day period.

	<i>Acmaea jamaicensis</i>		<i>Acmaea leucopleura</i>
	High	Low	
<i>n</i>	5	4	11
Total no. of observations	50	40	130
Total no. of moves	11	11	70
Daily displacement			
Total (\bar{x} cm \pm SE)	0.8 \pm 1.2	0.7 \pm 1.5	1.6 \pm 2.3
Range (cm)	0-4.3	0-13.3	0-8.2
Vertical (\bar{x} cm \pm SE)	-0.1 \pm 0.7	0.5 \pm 1.3	—

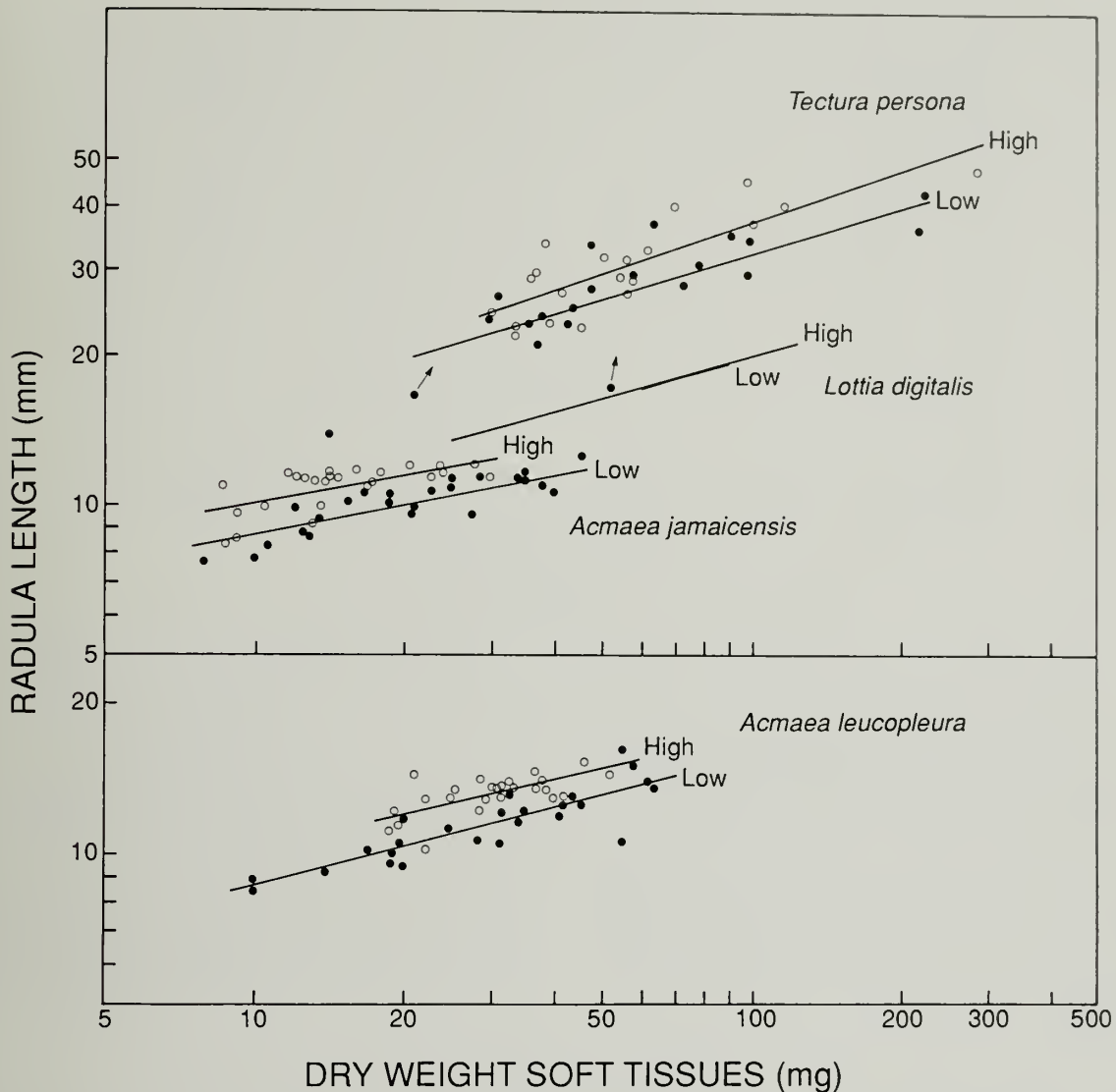


Figure 1

Comparison of radula lengths in high and low intertidal-level *Tectura persona*, *Lottia digitalis*, *Acmaea leucopleura*, and *A. jamaicensis*. High- and low-level data sets differ significantly for *T. persona* (F -ratio = 6.6, $P = 0.01$, ANOVA), *A. jamaicensis* (F -ratio = 18.7, $P < 0.001$, ANOVA), *A. leucopleura* (F -ratio = 33.6, $P < 0.001$, ANOVA), but not for *L. digitalis* (F -ratio = 0.03, $P = 0.87$, ANOVA); $n = 20$ for each set of *T. persona* and 25 for each set of each of the other species. Points omitted from *L. digitalis* regressions for clarity. Regression statistics for these curves are given in Table 1. Slopes of the regressions are not significantly different for any data set ($P > 0.50$, ANCOVA).

low, and increased through transfer of low ones to high, were not supported by the results. No significant effect on radula length was shown in low-level animals moved to a high level for 10 weeks (42.7 mm radula length as compared with 40.0 mm in the controls; $P > 0.05$, MCT), and high animals transferred to a low level for the same length of time unexpectedly showed a significant increase in radula length (53.0 mm after 10 weeks as compared with the control value of 46.2 mm; $P < 0.05$, MCT). Neither control set differed significantly with respect to

radula length from uncaged animals at the same tidal height at the end of the 10-week period (uncaged low = 41.3 mm and uncaged high = 44.5 mm, for animals of 148 mg dry tissue weight; $P > 0.20$ for each comparison; ANOVA). We concluded from this that there were no significant cage effects on radula lengths.

The results of the tide-tank experiment to assess the effects of time on change in radula length (Table 4) showed that high-level animals, when transferred to a low level, apparently underwent a shortening of their radulae until,

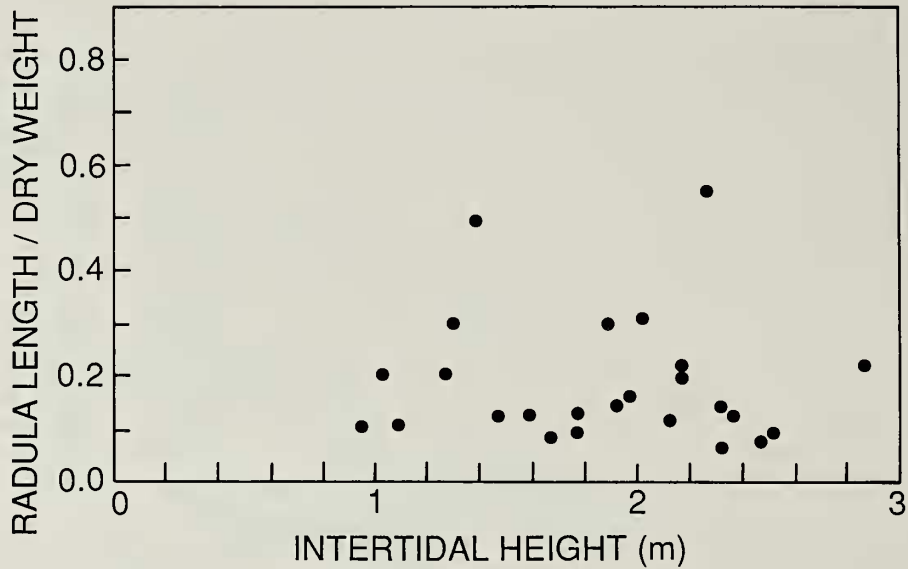


Figure 2

Relationship of the ratio of radula length over dry weight of soft tissues, to intertidal height occupied, in *Tectura scutum* from the west coast of British Columbia. Slope of the regression ($b = 0.003$) is not significantly different from zero ($P > 0.20$; t -test).

after 3 weeks, their radulae were significantly shorter than those of the controls (63.3 as compared with 73.0 mm, respectively; $P < 0.05$, MCT; measured at a common dry tissue weight of 440 mg at which the ANOVA was performed). However, after 7.5 weeks at a low level in the tide-tank, radula lengths of the experimental animals did not differ significantly from those of the controls (72.8 and 76.6 mm, respectively). The control animals showed some non-significant variation in radula lengths over the 7.5-week experiment (73.0–76.6 mm; $P > 0.05$, MCT).

DISCUSSION

Radula fraction, as defined by FISCHER-PIETTE (1935), has been frequently used as a means of comparing radula lengths in different-sized limpet species (ESLICK, 1940; BRIAN & OWEN, 1952; RAO & GANAPATI, 1967), variation in size supposedly being accounted for by using shell length as a correction factor. However, multiple regression analyses in the present study suggest that weight correction may more adequately ensure comparability of radula

Table 4

Effect of change in intertidal height occupied on radula lengths in the limpet *Tectura persona*. Translocation experiments were done using cages in the field and slate plates suspended at different "intertidal" heights in a tide-tank in the laboratory. "High" animals were collected from 4.3 m above zero chart datum and "low" animals from 2.6 m. Field cages were positioned at corresponding intertidal locations. Slate plates in the laboratory tide-tank were located at equivalent intertidal positions ("high," 0.89 m; "low," 0.55 m). The "common dry weight" is the factored dry tissue weight at which the ANOVAs were performed between high- and low-intertidal groups in order to eliminate size effects. Radula-length values were taken from the regression plot of radula length versus dry tissue weight for each set of data at the common weight indicated; n values are given in parentheses.

Study location	Season	No. weeks treatment	Common weight (dry mg)	Radula length (mm) after treatment:			
				High kept at high: Control	High kept at low	Low kept at low: Control	Low kept at high
Field	Autumn	10	148	46.2 (18)	53.0 (18)	40.0 (18)	42.7 (11)
Tide-tank	Summer-autumn	0	440	74.5 (10)	73.9 (10)	—	—
		3	440	73.0 (12)	63.3 (8)	—	—
		7.5	440	76.6 (25)	72.8 (16)	—	—

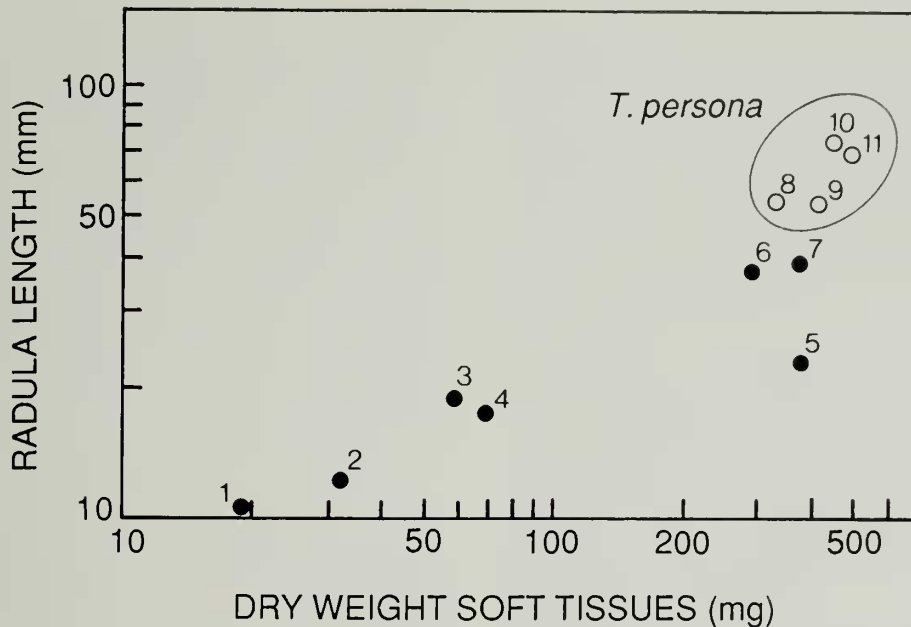


Figure 3

Relationship of radula length to dry tissue weight in several acmaeid and lottiid limpets from the west coasts of British Columbia and Barbados. Only large individuals from the upper portion of the intertidal range were chosen. Numbers by each point indicate the species, n value and, for species not part of the present study, geographical location as shown below. Numbers 8-11 represent populations of *Tectura persona* from different geographical areas in British Columbia. 1: *Acmaea jamaicensis*, $n = 25$; 2: *A. leucopleura*, $n = 25$; 3: *A. antillarum*, $n = 25$; 4: *Lottia digitalis*, $n = 25$; 5: *L. pelta*, $n = 50$ (DEHNEL, 1978); 6: *Tectura scutum*, $n = 25$; 7: *T. scutum*, $n = 50$ (DEHNEL, 1978); 8: *T. persona*, $n = 25$, Bamfield, B.C.; 9: *T. persona*, $n = 25$, Lighthouse Park, B.C.; 10: *T. persona*, $n = 25$, Botanical Beach, B.C.; 11: *T. persona*, $n = 50$, Bowen Island, B.C. (DEHNEL, 1978).

lengths than length correction, at least in *Tectura persona*. In a study of morphological variation in Pacific coast limpets, part of which included a comparison of radula length to various body dimensions, DEHNEL (1978) also concluded that weight of body tissue was a more accurate measure of animal size than shell length.

Radula length is a variable component both within (BRIAN & OWEN, 1952; RAO & GANAPATI, 1967) and between limpet species. Its magnitude may change in response to, or be correlated with, environmental factors such as intertidal height, desiccation, and geographical location. The variability in radula length between species is illustrated in a comparison of radula length versus dry tissue weight in a variety of lottiid and acmaeid limpets from the west coast of North America and Barbados (Figure 3). These data were taken from various literature references and from collections of *Tectura persona* around the British Columbia coast. They include only large animals at the high parts of their intertidal ranges. They show not only a wide scatter in weight-corrected radula lengths among the different species, but also some marked geographical differences. For example, at a common dry tissue weight of 425 mg, radula lengths of several populations of *T. persona* differ by as much as 37%. Thus, radula length seems to be a species-specific characteristic that can show striking geographical differences within a species. Effects on radula wear that might produce such differences include

feeding rate, type of food eaten, substrate texture, and hardness of the radula cusps (see RUNHAM & THORNTON, 1967). Food abundance and availability, which vary with intertidal height both within and between geographical areas, may also be important. At present, there is little knowledge of how these factors affect radula wear in limpets.

The results of the present study suggest that the radula-lengthening effect of increased intertidal height may be a species-dependent tendency relating to how strictly individual limpets remain in a certain intertidal position. Differences in weight-corrected radula length were highly significant in *Acmaea leucopleura* and *A. jamaicensis*, species that demonstrate a high fidelity to "homesite" locations. To a lesser degree, significant differentiation in radula lengths was also exhibited by high- and low-level *Tectura persona*. Although this species is not generally considered a homing one (VILLEE & GROODY, 1940; BRANCH, 1981), daily movements appear to be slight (unpublished observations) and are mostly in the horizontal plane (VILLEE & GROODY, 1940). *Tectura persona* thus appears to occupy a relatively constant position on the shore. Similar observations have been made on *Patella vulgata* (BRIAN & OWEN, 1952; EBLING *et al.*, 1962; VERMEIJ, 1972), a species that also exhibits differences related to intertidal height in relative radula length. In comparison, no significant difference in weight-corrected radula length was shown by high-

and low-level *Lottia digitalis* (Table 2). This species shows no (VILLEE & GROODY, 1940; HAVEN, 1973) or only slight (FRANK, 1964; GALBRAITH, 1965; MILLER, 1968; BREEN, 1971) homing tendencies and, in addition, shows dispersal in response to crowding (FRANK, 1965; BREEN, 1972), moves vertically in response to tides and wave splash (MILLER, 1968; FRANK, 1965), and undertakes seasonal vertical migrations (FRANK, 1965; HAVEN, 1971; BREEN, 1972). Similarly, differentiation of radula length with respect to intertidal height was lacking in a population of *T. scutum* (see Figure 2). This is a free-roaming species (TEST, 1945) that moves into and out of tide-pools, thus confronting variable feeding opportunities, and it shows no evidence of homing behavior (VILLEE & GROODY, 1940).

These patterns of differentiation in radula lengths support the argument advanced by BRIAN & OWEN (1952) and later by RAO & GANAPATI (1967) that a decrease in radula wear in animals that live consistently at high intertidal levels, and therefore possibly experience more restricted feeding time, is chiefly responsible for the increase in radula fraction from low to high intertidal levels. Limpets have generally been observed to feed only when immersed, when emersed but on wet surfaces, or when splashed by waves (ORTON, 1929; SUTHERLAND, 1970; BOYDEN & ZELDIS, 1979; KITTING, 1979; HULINGS, 1985), although foraging behavior is variable even within a species (LITTLE & STIRLING, 1985; LITTLE *et al.*, 1988). The idea of decreased feeding time being chiefly responsible for increased radula-fraction in high intertidal-level limpets is supported by the observations of KOCH (1949) on South African *Patella* spp. This author recorded higher length-corrected radula lengths in species inhabiting drier parts of the shore where feeding excursions were limited. Similarly, more rapid relative growth rates shown by several limpet species in the lower intertidal area as compared with the upper may possibly be attributed to more food and greater availability of foraging time in the lower regions (FISCHER-PIETTE, 1935; SUTHERLAND, 1970; LEWIS & BOWMAN, 1975; PHILLIPS, 1981).

The results of the tide-tank translocation experiment also suggest that feeding opportunity (including feeding time, food availability, and food attractiveness) may be important in controlling radula length. Thus, the shortening of the radula in high-level animals 3 weeks after transfer to a low-level position in the tide-tank may have been caused by rapid feeding in animals confronted with abundant food on the slate plates. With subsequent depletion of food, the radula was worn less and showed an increase in relative length. At the end of the experiment the slate plates were barren of food and dissections of animals showed that both high- and low-level sets had empty stomachs.

As attractive as this explanation may be, however, it is not supported by the results of the field experiment. Diatoms were abundant throughout the intertidal region in December (particularly at the high levels) at the termination of the field experiment, and dissections of freshly

collected field animals revealed that most had full guts. The lengthening of the radula evidenced by high-level animals moved to a low level was not reflected in the low-level control group, which had radulae of similar lengths to uncaged field animals at the same intertidal level. Mortality rates were high (40–63% in all experimental groups; no size-specific mortality), suggesting that handling and other stresses may have been involved. Attempts to move limpets from their natural substrata to other locations, with either the same substrata or an artificial one in the laboratory, usually resulted in slow reattachment and high mortality. Thus, the most logical means of testing the influence of tidal height on radula length, namely to effect a change in radula length through a manipulation of tidal height, provided unclear results in this study.

Although the physical limits on radula growth in limpets are not known, an individual that is not using its radula (and, thus, presumably not wearing it away) may continue to produce a radula until a "radular capacity" is maximized. It appears that in large specimens of *Tectura persona* maximum "capacity" is approximately 2.5 times the shell length, a ratio comparable to that found in high-level *Patella vulgata* (EVANS, 1947). This abundance of radula can be thought of as an investment to be drawn on under improved feeding conditions. At present, there are no reliable estimates of radula replacement rates for limpets (see ISARANKURA & RUNHAM, 1968). However, if radula replacement rate is consistent regardless of wear, this may explain the marked tide-level differences in relative radula lengths in species such as *T. persona* and *Acmaea leucopleura*, whose extensive vertical ranges put part of each population into the high intertidal zone where opportunity for feeding is presumably lessened. Thus, the greater the tendency for limpets to remain at a specific height for extended periods, the greater will be the lengthening effect on the radula. Presumably, as suggested by the data from the tide-tank experiment, once food-deprived limpets resume normal feeding, radula wear increases and the extensive radula built up during deprivation is worn away.

This analysis will remain speculative until major questions can be answered relating to the effect on radula length of differences in feeding rate and, in turn, to the amount of food required to meet energy demands. Energy requirements of limpets are undoubtedly different at different intertidal levels (see MCMAHON & RUSSELL-HUNTER, 1977) and may vary seasonally. Food supply is known to vary seasonally in both type and amount, and these variations will affect feeding rates and, thus, radula wear. Fluctuations in the type and density of food and general patchiness in distribution of food may explain the low correlation coefficients between radula length and morphometric parameters exhibited by low-level (*i.e.*, more actively feeding) limpets (see data for *Tectura persona*, Table 1). Studies are now underway to determine the effect of intertidal position on feeding rates and radula replacement rates in *T. persona* to help answer some of these questions.

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